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The bionomics of *Spindasis greeni* Heron, 1896 and a review of the early stages of the genus *Spindasis* in Sri Lanka (Lepidoptera: Lycaenidae)

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Abstract. The occurrence of *Spindasis greeni* in Sri Lanka and its status as a species is confirmed more than 100 years after the original description. Additional descriptive notes of the male based on fresh material are presented. The female, the immature stages and behavior are documented for the first time and its distribution mapped. For comparison, the immature stages of *S. vulcanus fusca*, *S. ictis ceylonica* and *S. elima fairliei* in Sri Lanka are described for the first time and their larval food plants and ant associations identified.

Keywords: *Spindasis*, immature stages, Sri Lanka, Lycaenidae, ant associations, *Crematogaster*, *Tapinoma*.

Introduction

Heron (1896) described *Spindasis greeni* (subfamily Theclinae, tribe Aphnaeini) from a single, worn specimen of a male obtained by E. E. Green in Sri Lanka. It was accepted as a valid species by some authors but not by others. de Nicéville & Manders (1899) listed it as *Aphnaeus greeni* but noted that de Nicéville had examined the specimen and preferred to express no opinion regarding its validity as a distinct species. Swinhoe (1911–1912) listed it as *A. greeni* and re-described it from the holotype. Ormiston (1918) listed it as *A. greeni* and stated that Evans thought it was an aberration of *A. [vulcanus] fusca*. Ormiston (1924) listed it as *S. greeni* (along with the synonym *S. lunulifera* ab. *greeni* Riley) and stated that Riley would not create a new species in this genus from a single specimen because aberrations are so common in the genus. He further stated that the genitalia prove its connection with *S. lunulifera* but did not provide any description or illustration to support this statement. Evans (1927, 1932) and Woodhouse (1949) thought it was *S. ictis ceylanica* [sic]. d'Abrera (1986) wrote "I am not certain that this is a 'good' species. The unique holotype (male) is probably an aberration of another local species – precisely which species is hard to tell because both surfaces are so weakly marked." d'Abrera (1998) did not list it. H. Gaonkar (pers. comm.) listed it as an endemic species for Sri Lanka despite some reservations since he also noted "The type - (male) HOLOTYPE - of this species is unique. I am uncertain whether the specimen actually belongs to a distinct species described as *greeni* by Heron or an aberration of another species. New materials will be needed."

Seven species of *Spindasis* are reported from Sri Lanka: *S. vulcanus fusca* (Moore, 1881), *S. schistacea* (Moore, 1881), *S. nubilus* (Moore, [1887]), *S. ictis ceylonica* Felder, 1868, *S. elima fairliei* Ormiston, 1924, *S. lohita lazularia* (Moore, 1881), and *S. greeni*. All are endemic at least at the subspecies level except for *S. schistacea* and *S. lohita lazularia*. Fourteen species of *Spindasis* and two related *Apharitis* species are found in India, to which Sri Lanka is zoogeographically related: (1) *Apharitis acamas hypargyros* (Butler, 1886), (2) *A. l. lilacinus* (Moore, 1884) (3) *Spindasis abnormis* (Moore, 1884), (4) *S. e. elima* (Moore, 1877), *S. e. uniformis* (Moore, 1882), (5) *S. elwesi* Evans, 1925, (6) *S. e. evansii* (Tytler, 1915), (7) *S. gabriel* (Swinhoe, 1912), (8) *S. i. ictis* (Hewitson, 1865), (9) *S. maximus* (Elwes, 1893), (10) *S. nipalicus* (Moore, 1884), (11) *S. lohita lazularia* (Moore, 1881), *S. l. himalayanus* (Moore, 1884), *S. l. zoilus* (Moore, 1877), (12) *S. r. rukma* (de Nicéville, 1888), (13) *S. rukmini* (de Nicéville, 1888), (14) *S. schistacea* (Moore, 1881), (15) *S. syama peguanus* (Moore, 1884) and (16) *S. v. vulcanus* (Fabricius, 1775) (provisional list supplied by K. Kunte, pers. comm.).

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Many Lycaenidae are known to exhibit larval-ant associations (Fiedler, 2006; Pierce *et al.*, 2002). In India and Sri Lanka, the members of the genus *Spindasis* are also considered to have similar associations (Woodhouse, 1949). However, of the 16 species of *Spindasis* recorded from these two countries, the early stages of only 3 species have been recorded: *S. lohita* (Marshall & de Nicéville, 1890; Green, 1902; Kershaw, 1907; Bell, 1919, Igarashi & Fukuda, 2000), *S. vulcanus* (Bell, 1919; Sidhu, 2010) and *S. abnormis* (Bean, 1968). The larva of *S. lohita* is reported to often build shelters (Kershaw, 1907; Bell 1919) and to often feed at night (Kershaw, 1907; Green, 1902; Igarashi & Fukuda, 2000). In the larval and pupal stages, all three species are associated with *Crematogaster* ants and additionally, with a species of *Pheidole* for *S. vulcanus* (Marshall & de Nicéville, 1890). The nature of the association, whether obligate or facultative, has not been reported in sufficient detail. As described in the current paper, the larvae of some species can reach the adult stage successfully in the lab without attendant ants. We speculate though that the presence of ants is necessary in the field to elicit oviposition by the female as has been shown for some other species (Pierce *et al.*, 2002). Each of these three species was recorded feeding on the leaves of more than one species of plant, sometimes from widely different families. This dependence on ants has evolved in at least one species to aphytophagy: *S. takanonis*, which is found in Japan, is completely aphytophagous, depending on its attendant *Crematogaster* ants to feed it mouth to mouth (Igarashi & Fukuda, 2000). Overall, the tribe Aphnaeini is known as a clade whose component species have particularly tight relationships with ants (Heath, 1997).

In April 2008, Nadeera Weerasinghe took several photographs of a butterfly ovipositing on a dead tree at the top of World's End in Horton Plains (Fig. 1a). Some photographs were forwarded to the authors who immediately recognized that it was an image of *S. greeni*. This was only the second sighting ever of *S. greeni*. A first attempt to locate the butterfly immediately after this did not succeed, but in March 2012 we were able to return to the location and located several males, females, eggs, pupae and a single larva.

Morphological evidence for specific distinctness

Specimens examined

Male holotype in NHM (London): [Label: Type/ Pundalaya [Feb.] G.E. Green 91-150./30/Pdo. 2/ [blank blue label] (Figs. 1b, c). Additional new specimens: 13 iii 2008 – 1♀, World's End (6.78092N, 80.79423E, 2100 m asl), Horton Plains; 24 iii 2012 - 1♂, 1♀ mating pair, Road B508, km 28 (6.79769N, 80.83039E, 2100 m asl), Horton Plains; 24 iii 2012 - 1♂, mini-World's End (6.78859N, 80.80174E, 2090 m asl), Horton Plains; 25 iii 2012 – 1♂, mini-World's End, 1♂, 1♀ mating pair, between mini-World's End and World's End (6.7288N, 80.79659E), Horton Plains. 1♂ and 1♀ to be deposited in the Sri Lanka National Museum.

Where information on the duration of developmental stages is given, these data were obtained in rearings at ambient temperatures (25–31°C) at Bandarakoswatte (07.37.01N, 80.10.57E), 70 m asl, North Western Province, Sri Lanka. Conventions used (applied to both the larva and the pupa): Segments are numbered S1 to S14 (S1—the head; S2 to S4—the 3 segments of the thorax; S5 to S14—the 10 segments of the abdomen). In the photographs, the head is on the left.

Comparison of newly collected males to the holotype

The somewhat worn holotype male was described by Heron (1896) and re-described by Swinhoe (1911–1912), and though both authors described the abdomen, it is now missing from the specimen. The newly acquired fresh specimens agree with these descriptions except for the following points: a) Forewing upperside: band along termen narrow at the tornus and wider at the apex, and continues more narrowly along the costa; band black or violet-brown depending on angle of view; color of remainder of wing depends on the angle of view—ranging from pale grayish blue to bright iridescent blue (Fig. 1d) to purplish blue (Fig. 1e); in all views, there are sparsely scattered pale grayish-blue scales from the base of the wing to the median line (Heron described them as "pale lilacine blue scales"); discocellulars and the radius clothed with black scales; dorsum lined with much longer pale brown hairs than the termen where the cilia are more densely packed. b) Hindwing upperside: color of iridescence between veins Rs and CuA_2 depends on the angle of view and varies from purplish-blue to bluish-gray (Fig. 1e); brownish-gray above vein Rs and below CuA_2; clothed at base and discal area with long pale brown hairs similar to those on the dorsum of forewing; anal fold densely packed with similar hairs. c) Forewing underside: ground color pale brownish-pink [not ochreous brown] with a pearly sheen; markings reduced but all are speckled with silver (Heron reported few); submarginal spots clearly visible (not traces) but diffuse. d) Hindwing

Figure 1. Adult *S. greeni* butterflies from Sri Lanka. **a)** Female, ovipositing on dead tree. **b)** Male, holotype, underside. **c)** Male, holotype, upperside. **d)** Male, upperside. **e)** Male, upperside. **f)** Male, underside, tails missing. **g)** Male, close up of tails, underside. **h)** Female, upperside. **i)** Female, underside, typical sitting posture. **j)** Female, close-up of tails, upperside. **k)** Female, close-up of tails, underside. **l)** Mating pair, male on the left. **m)** Male genitalia with aedeagus removed, lateral view. **n)** Aedeagus, lateral view. **o)** Distribution map of *S, abnormis* in India (red squares) and of *S. greeni* in Sri Lanka (black square).

underside: band between discal and submarginal bands clearly marked, not obscure; ground color darker shade of the forewing underside (brownish-pink); all markings with silver; small orange patch at base of each tail, often obscure or missing on the shorter tail. In both forewing and hindwing, ground color somewhat darker distally and the silver markings within the bands variable in intensity. Thorax and abdomen: black dorsally with salmon-colored scales laterally and ventrally that match the ground color of the underside of the wings. Antennae: outside edge black with white spots and bright orange at the tip; inner edge same color as underside of hindwing (Fig. 1f). Tails: Heron did not describe any tails though Swinhoe noted that the tails were broken. There are two pairs of tails: 1) 1 pair at CuA_2, 0.5 mm long, tip white, black in the middle, orange at base; 2) 1 pair at 1A+2A, 2 mm long, similarly colored (Fig. 1g) (2 specimens measured, both same length).

Wingspan 24 mm; forewing length along the costa 14 mm (2 specimens measured, both the same). Heron recorded the wingspan of the holotype specimen as 35 mm and Swinhoe as 1-3/10 inch [33 mm]. Since the holotype male was recorded as being much larger than the specimens we obtained, we re-measured the holotype male and found it to be 28 mm apex to apex, and 15 mm right forewing length.

First description of the female

Termen of forewing slightly more concave than that of the male. Forewing upperside: Ground color light bluish-gray with a silvery iridescence, gradually grading into grayish-black at the apex and along the termen towards the tornus; discal cell and cells below M_3 densely covered with scales, less so above M_3. Discocellulars and anterior portion of cubitus clothed with black scales which continue partway up veins M_1, M_2, M_3 and R_5; dorsum with fine long grayish-blue hairs decreasing in length towards tornus; cilia white with base gray; ground color changes depending on angle of light from bluish to grayish.

Hindwing upperside: entire wing iridescent light bluish-gray; area above vein Rs lightly dusted with bluish-gray scales; long light bluish-gray scales along the base of the wing, the discal cell and along the anal fold; the hairs in the anal fold near the tornus reddish-purple; diffuse marginal black line from veins Rs to CuA_2; two pairs of tails—1) 1 pair at CuA_2, 1 mm long, 2) 1 pair at 1A+2A, 3 mm long (2 specimens measured, both the same). Both pairs of tails tricolored as per the male; both pairs of tails longer than those of male (Figs. 1h, j). Forewing and hindwing underside: similar to the male though markings appear to be less pronounced (Figs. 1i, k). Wingspan: 26 mm; forewing length 16 mm (2 specimens measured, both the same).

Differential diagnosis

Heron (1896) compared the male of *S. greeni* to the male of *S. abnormis* from the Western Ghats in India (Moore, 1883; Bean, 1968; Lovalekar *et al.*, 2011), the species to which he thought it is most similar in appearance. However, since he had only a single worn specimen, he was unsure of some of the morphological features. Our findings confirm the similarities (both taken at higher altitudes and with reduced markings) and differences (shape and color of wings, greatly reduced and interrupted markings on the underside in *S. greeni*) that Heron pointed out and also confirm that the male *S. greeni* does not have the large ochreous-brown anal lobe on the upperside of the hindwing that is so prominent in male *S. abnormis*.

Comparing specimens in the NHM London and the description in Swinhoe (1911–1912), we observed the following differences in the females of the two species: the female of *S. greeni* lacks the dull red anal lobe and the discal cell-end bar on the upperside of the hindwing which are present in female *S. abnormis*. As in the male, the markings on the underside are interrupted and significantly reduced in *S. greeni*. *S. abnormis* is considerably larger as reported by Moore (1883): ♂ 1.5 inches (38 mm) and by Swinhoe (1911–1912): ♂ 1.6 inches (40.6 mm) and ♀ 1.7 inches (43 mm).

The 5 males and 4 females of *S. greeni* observed in the field exhibited minimal variation. *S. greeni* is morphologically distinct from all other Sri Lankan *Spindasis*.

The genitalia of two males were examined and compared to those of *S. abnormis* described and illustrated by Bean (1968) and to Sri Lankan species of *Spindasis* illustrated by Woodhouse (1949). The genitalia of *S. greeni* (Figs. 1m, n) are distinct from *S. abnormis* in the following respects (in lateral view): 1) each lobe of the uncus is broader and more obtuse at the apex; 2) the costa of the valve is deeply curved (in *S. abnormis*, it is only slightly curved); 3) the apex of the valve is beak-like with 3 distinct protuberances along the dorsal edge (in *S. abnormis*, the valve is deeply indented on the dorsal edge to form a cleft posterior to the apex); 4) the suprazone of the aedeagus is distinctly bent upwards and slightly curved at the tip (the suprazone of *S. abnormis* is straight); 5) the subzone of the aedeagus is convex on the ventral margin (that of *S. abnormis* is straight); and 6) the vinculum is much narrower. The genitalia of *S. greeni* are also distinct from all other Sri Lankan *Spindasis*, but are most similar to those of *S. elima fairliei* (which Ormiston referred to as *S. lunulifera*).

These observations show that *S. greeni* is not a subspecies of *S. abnormis* or a different phenotype of any other species of *Spindasis* as suggested by some authors. Given the morphological similarities between *S. greeni* and *S. abnormis* and the close zoogeographic relationship of the southwestern sector of Sri Lanka with the Western Ghats in India (Myers, 1988; Myers *et al.*, 2000), it is possible that they are closely related phylogenetically. Molecular studies are needed to test this idea.

Distribution and habitat

Horton Plains is located in the south-western sector of the island and though it has some affinity with the Western Ghats, it is also unique. The distribution of species pairs such as *S. abnormis* in the Western Ghats and *S. greeni* in Horton Plains is not unusual (Fig. 1o) since there are similar instances for other taxa. For example, in an analysis of the vascular plant flora, Gunatilleke & Pethiyagoda (2012) found that 9% of Sri Lanka's plant species and 12% of its endemics occur in Horton Plains and that 28% of the non-endemic species of Horton Plains are found only in Sri Lanka and the southern mountain ranges of the Western Ghats. Mani (1974) reported that the Turkmenian (Palaearctic) elements of the Indian flora and fauna were confined to the higher Himalayas and occur as isolates on the Eastern and Western Ghats and "even in the hills of Ceylon [Sri Lanka]." Among birds, there are several "species pairs": for example, *Saxicola caprata* is a breeding resident in Horton Plains, and is also found, along with several other species of *Saxicola*, in the Western Ghats. In butterflies, *Udara singalensis* and *U. lanka* are endemics that are found in Horton Plains, while the related *U. akasa* is found in Horton Plains as well as the Western Ghats.

Heron (1896) reported that the holotype male had been taken "near Pundaloya, on the summit of the great western range of hills in Ceylon, at this point attaining a height of about 6000 feet [1828 m]." He also listed "Hab." as "Pundaloya" which was repeated by subsequent authors. However, it is unlikely that Pundaloya (which is where Green was stationed) is the true location of the original specimen as it is located on a plateau at a much lower elevation (1050 m asl). However, near Pundaloya there is a mountain called the Great Western Mountain (6.96451N, 80.69321E) which reaches 2200 m asl at its peak. It is very likely that this is the location where Green caught the original specimen.

Figure 2. Habitat of *S. greeni* from Sri Lanka. **a)** First author at World's End, escarpment visible at left. **b)** Typical habitat with stunted vegetation; dead tree on which the larva and pupae were found to the right.

The sighting in 2008 was at World's End in Horton Plains. The sightings in 2012 were at World's End, mini-World's End and on the Ohiya Road (B508 at km 28) in Horton Plains (all at approximately 2100 m asl). The locations in Horton Plains are about 20 km crow's flight distance from the Great Western Mountain, and though they are part of the same mountain complex, they are not contiguous and are separated by a plateau with an elevation of about 1600 m asl.

Horton Plains is a unique habitat in Sri Lanka—it is a highland plateau at the southern edge of the central mountain massif, 31 km² in extent. On the south-eastern side, it is bounded by the World's End escarpment which is about 800 m high (Fig. 2a). Road B508 also runs along the edge of the escarpment. Rainfall is moderate (around 2000 mm per year); mean annual temperature is 15°C (range: 0 to 28°C). Cloudy, misty days prevail for most of the year and there are strong winds during the south-west monsoon (May to July). The vegetation comprises Tropical Montane Cloud Forest (80%) and Wet Patana Grasslands (20%), and the trees are generally stunted (about 12 m tall). *Callophylum walkeri*, *Syzygium rotundifolium*, *Symplocos elegans*, *Cinnamomum ovalifolium*, *Glochidion pycnocarpum* and *Neolitsea fuscata* are major tree components of the forest (Gunatilleke & Pethiyagoda, 2012; Gunatilleke *et al.*, 2008). Canopy die-back is an extensive problem in the park. Though first reported in 1978, the reason for the die-back is still unknown though several hypotheses have been advanced (Werner, 1988; Adikaram *et al.*, 2006). Fifty-five species of butterflies have been recorded from the park though only 23 species are considered to be resident (van der Poorten, 2012). The others simply fly through the plains during their migrations. *S. greeni* was found on the edge of the escarpment in areas with stunted vegetation and dead trees (Fig. 2b).

Though *S. greeni* has been reported from only Horton Plains and the Great Western Mountain, there are other locations in Sri Lanka that are also covered by Tropical Montane Cloud Forests (TMCF) (Gunatilleke & Pethiyagoda, 2012) where *S. greeni* might be found. Hakgala Strict Natural Reserve and Pedro Forest Reserve have a similar climate and vegetation to Horton Plains though there is no information as to whether or not the attending ant, *C. rothneyi* or another species of *Crematogaster* is found there. The Peak Wilderness Sanctuary above 1500 m asl, the Knuckles Conservation Area and the peak of Namunukula are also TMCFs (Gunatilleke & Pethiyagoda, 2012) but have slightly different climatic conditions and vegetation; again, there is no information about the ant species found there.

Faunistic data (sightings by the authors unless otherwise indicated): March 13, 2008 – 1 ♀ observed and photographed ovipositing on a dead tree at World's End in Horton Plains (N. Weerasinghe, pers. comm.); March 24, 2012 –1♂and two eggs at Mini-World's End (H. D. Jayasinghe & C. de Alwis, pers. comm.) and one mating pair on Ohiya Road (B508) at Km 28; March 25, 2012 (with H. D. Jayasinghe & C. de Alwis) – one mating pair, one larva and four pupae between Mini-Worlds' End and World's End; 1♂ at Mini-Worlds' End.

Adult behavior and associated ants

Like others in the genus, both sexes fly very rapidly and are difficult to follow once airborne. However, they frequently settle on the top of the stunted trees that are common in Horton Plains but seldom descend to the ground. They are best observed through binoculars. Once settled (often with the head pointing down), they frequently spread their wings open halfway and slant their bodies to bask in the sun to warm up. Frequent warming up is essential at these altitudes to keep body temperature optimal for flight—the ambient temperatures here are often well below 10°C in the mornings and seldom exceed 20°C.

Though no *S. greeni* butterflies were observed feeding on floral nectar, several plants such as *Ageratina riparia*, *Hedyotis lessertiana*, *Vernonia wightiana* and several species of *Knoxia* were in bloom at that time. In India, Bean (1968) recorded *S. abnormis* feeding on many different flowers.

Courtship was not observed but two mating pairs were seen (Fig. 1l). In both cases, both individuals were in pristine condition and had presumably just emerged. When the pair in copula was disturbed, they flew together to a point just a few meters away. They repeated this process of flying and settling a few more times.

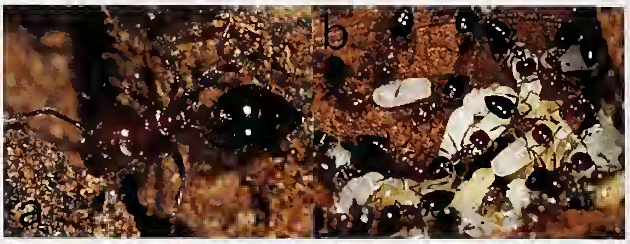


Figure 3. *Crematogaster rothneyi*: ants associated with *S. greeni* in Sri Lanka. **a)** Worker ant. **b)** Ants with their brood.

A female was observed ovipositing on the bark of a dead tree in March 2008. On March 25, 2012, eggs were also found on the bark of a dead tree, in a small crevice but still visible from the outside. Eggs were laid singly or in batches of 2–3 and were found only on trees that harbored the ant *Crematogaster rothneyi* Mayr, 1878 (Formicidae: Myrmicinae) (Figs. 3a, b). It is not known how the female is able to determine the presence of ants because not all dead trees harbor a colony and ants were not visible on the surface. No ants were observed attending the eggs.

There are 13 species of *Crematogaster* recorded from Sri Lanka (Dias, 2002). *Crematogaster rothneyi* is widespread in southern Asia and has been reported from all over India (Bingham, 1903) (*C. r. rothneyi*, *C. r. civa* Forel, 1902), from Haputale in Sri Lanka (*C. rothneyi haputalensis* Forel, 1913) (Forel, 1913) and from Kampong Chnang in central Cambodia (antweb. org, 2012; subspecies not identified), from Rangoon, Burma (Wheeler 1927; subspecies not identified) and from the Punjab province in Pakistan (Umair *et al.*, 2012). The majority of *Crematogaster* species in India build brown papery nests made of vegetable fiber on a large tree but some species build nests in hollows of trees, in the ground or under stones. The same species may build a different kind of nest in different parts of the country (Bingham, 1903). In India, *C. rothneyi* has been reported as nesting in soil, in crevices in the walls of buildings (Ayyar, 1937) or as nesting in a "carton" nest (presumably a brown papery nest) on the trunk of a large tree in Tamil Nadu (Tiwari, 1999). In Sri Lanka, the distribution of *C. rothneyi* is unknown though the type of *C. rothneyi haputalensis* was recorded from Haputale at 1500 m asl. There are no reports of its nesting habits.

In this study, the ants were found in a large colony, inhabiting dead trees where they used the galleries already established by other insects, possibly coleopterans. No ants were visible on the surface of the tree but when the tree was pounded upon quite vigorously many ants moved out to the surface of the bark. Underneath the bark, a colony was visible with a large number of ant eggs, larvae, pupae and workers in the crevices. Of the 8 stumps examined, a large colony of *C. rothneyi* was found in 5 of them and no other ants were observed. There is no information on the ant fauna of Horton Plains and the ecology of *C. rothneyi* is not known. Umair *et al.* (2012) reported that it was found in Pakistan in grasslands, fields of maize and wheat, apple orchards and pine trees. It appears to be an ecologically dominant species where it occurs.

Immature stages of *S. greeni*

Egg: pale green when first laid, turning beige within one day and darker brown just before hatching, dome-shaped and finely sculptured with hexagonal and pentagonal depressions, somewhat reminiscent of the surface of a golf ball, similar to eggs of other species of *Spindasis* (Fig. 4a). 1st instar: ate only top portion of eggshell; larva very active; length 3 mm; head black, not retracted; body ground color light purplish-pink, an indistinct light bluish-gray band dorsally fading towards the posterior end and absent beyond S10, S2–S3 dark purple dorsally and lighter colored laterally, S4–S7 with more or less oval spots on either side of the dorsal line embedded within the dorsal band, S2–S14 with long silvery-pink hairs laterally, 2 per segment from S4–S12, more numerous on anterior segments and anal plate. Dorsal nectar organ (DNO) on S11 appears as a darker reddish slit, S12 with a pair of rudimentary tentacle organs (TO), anal plate grayish-pink. Mouthparts normal (Fig. 4b). 2nd–4th instars not seen.

Final instar, prepupation: typical *Spindasis* shape; length 16 mm; head black, not retracted; body pale yellowish-brown, dorsal line dark reddish-brown, an obscure more or less discontinuous reddish-brown subdorsal line, lateral line of similar color but broader and more distinct, dorso-ventral flange pink, tufts of setae at the center of each segment along the flange, DNO on S11, a pair of TOs on S12 with white rod-like eversible tentacles, opening of the tentacles lined with black hairs, dark brown patch on dorsum of anal plate surrounded by a ring of setae, spiracles obscure and small, yellowish-white, anterior edge of S2 with a series of fine long hairs, dorsum of S2 with a rhomboidal depression that is darker than the surroundings) (Figs. 4c–e). The larva just described was found underneath the bark of a dead tree with ants attending the whole body, indicating that the larva likely has pore cupola organs (Fig. 4f).

Pupa: typical shape of *Spindasis*, length 12–13.5 mm, width 3–5 mm; smooth, head pale cream-colored, prothorax reddish-brown with two dark rings (appearing like eyes) on the dorsum, mesothorax dark brown dorsally fading to a lighter shade subdorsally and laterally, metathorax lighter reddish-brown, wing buds and abdomen light brownish-yellow but darker on the dorsum, spiracles small, slit-like and brownish-red, S8–S11 with obscure dark circular areas surrounding the spiracles (Figs. 4g, h). Some pupae lighter colored (Figs. 4i, j). Attached by cremaster only, no girdle; weakly attached to the substrate. In the field, pupae were found on the ground under fallen debris and just underneath the bark in close proximity to an exit hole with the head pointing down. Ants also attended the pupa that was underneath the bark (Fig. 4k).

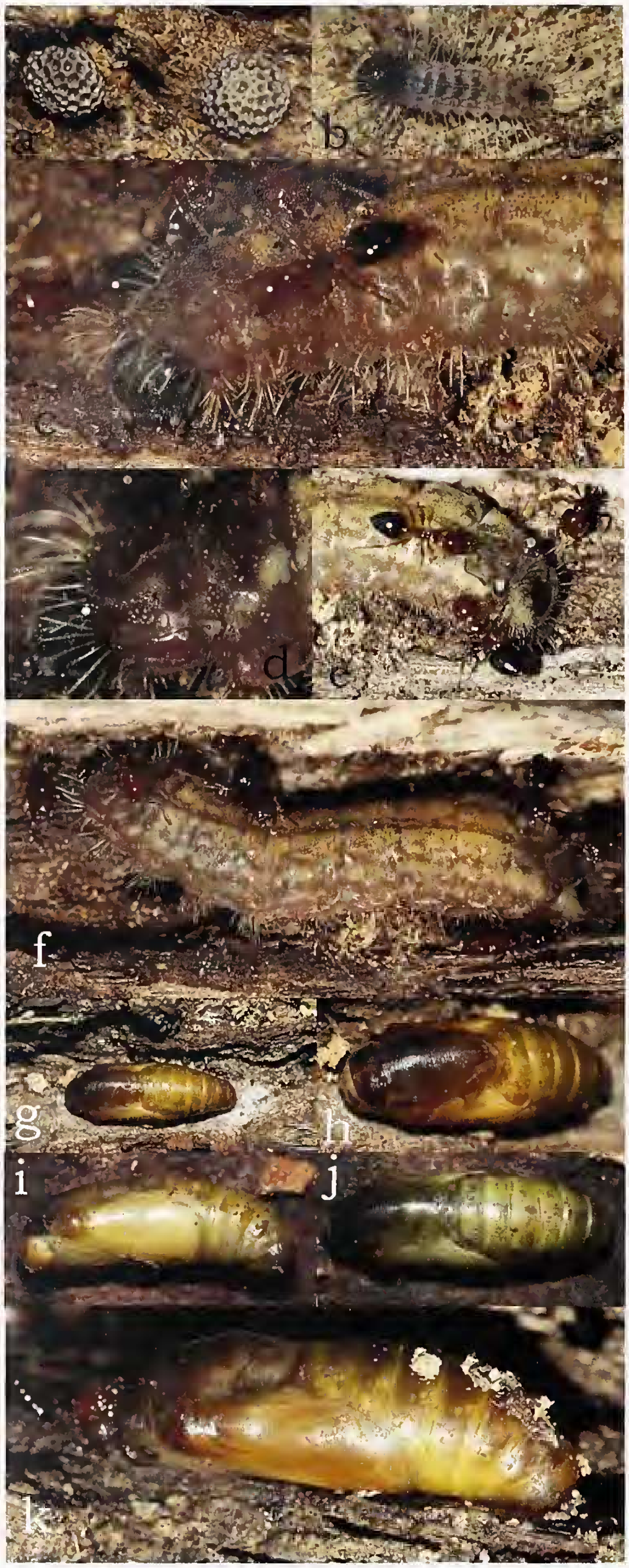
Duration of immature stages: egg more than 7 d; pupa more than 7 d.

Some thoughts about larval life-history of *S. greeni*

Though we have not been able to identify the exact association that *S. greeni* has with ants and have not been able to document the immature stages completely, we present the following information and speculations.

Several eggs and a single final instar larva were found in the field on dead trees within 1–2 m from the ground (heights above this were not examined); these dead trees all had colonies of *C. rothneyi* and moist decaying tissue within. In one of the trees examined, a larva was found just underneath the bark. After a few photographs of it were taken *in situ*, the larva moved and dropped into the dense undergrowth and could not be recovered for further study. No eggs or larvae were found on dead tree trunks that had dry, hard wood inside despite the presence of ants. During oviposition, the ants were not observed on the outside of the bark of the dead trees and we have not been able to determine how the adult female locates the presence of ants. The most likely mechanism is that the female (as has been shown in other obligate myrmecophiles) is able to recognize some of the many pheromones used by their host ants, and then finds trees with ant colonies (K. Fiedler, pers. comm.).

In the lab, we opened up a piece of dead wood to expose the ants and ant galleries and placed newly hatched larvae on the wood. The larvae moved very quickly from the surface, away from the bright light, into an ant gallery which was 2–3 mm wide. While moving, the larvae had no reaction to the ants present nor the ants to the larvae; both parties ignored each other. It was not possible to retrieve the larvae or make any records of them once they entered the dead wood, and careful inspection of the wood after 4 and 10 days did not reveal any larvae. We presume that they had died.



In the field, we observed ants attending the final instar larva and pupa, just underneath the bark within the galleries, but the exact nature of the relationship is not clear. The larva was attended by 5–10 ants which were spread over the entire body, but often concentrated around the DNO and the junction of S2–S3 from which the ants seemed to derive some nutriment. None of the ants were moving about excitedly as in the case of *S. vulcanus fusca* (see below) or as with *S. abnormis* (Bean, 1968) but were decidedly subdued. When the ants were near the DNO, the larva frequently everted the 2 TOs but no response from the ants was observed (though in other *Spindasis* such as S. *vulcanus fusca* this often excites the ants). The tree on which the larva was found had large (10–20 mm diameter) interconnected passageways that were of sufficient diameter for the movement of the larger, later instar larvae of *S. greeni* to forage and rest. However, the ant passages, which were connected to these larger passages, were smaller and would not have allowed a full grown larva to enter or exit. This shows that a later instar larva would not have access to the ant brood on which it may possibly feed. It is possible that the larva feeds on the ant brood in the early stages when it can move in and out of the brood chambers easily. However, in the lab, the first instar larvae paid no attention to the ant brood that was offered to them when they first emerged.

Another possibility is that the ants feed the larva mouth to mouth through trophallaxis, as has been reported for *S. takanonis* in Japan (Igarashi & Fukuda, 2000) or that the larva of *S. greeni* feeds on vegetation outside the dead tree. Other aphytophagous lycaenids have also been recorded as feeding on honeydew (Cottrell, 1984) or hemipterans. Further investigation is required to elucidate the feeding behavior of the larva of *S. greeni* and its association with the ants.

Review of the immature stages of species in the genus *Spindasis* in Sri Lanka

In addition to *S. greeni*, there are 6 other species of *Spindasis* in Sri Lanka. All members of the

Figure 4. Early stages of *Spindasis greeni* from Sri Lanka. **a)** Eggs. **b)** Larva, first instar. **c)** Larva, final instar, prepupation, anterior end, attending ants visible. **d)** Larva, as in (c), close up of S2–S3. **e)** Larva, as in (c), posterior end, attending ants visible. **f)** Larva, as in (c), attended by ants; photo rotated 90° counterclockwise from its natural position. **g)** Pupa, dorsal view. **h)** Pupa, same as (g), close-up. **i)** Pupa, lighter colored, dorsal view. **j)** Pupa, same as (i), lateral view. k) Pupa, *in situ* underneath bark, attended by ants; photo rotated 90° clockwise from its natural position.

tribe Aphnaeini whose life-histories are known are myrmecophiles and almost all obligately so (K. Fiedler, pers. comm.). Heath (1997) reported over 60 species of *Chrysoritis* from Africa with such an association. In Asia, only 3 species of *Spindasis* have been reasonably well-studied (*S. lohita*, *S. syama* and *S. takanonis*) and they also appear to be obligate myrmecophiles. However, the ant association has not always been carefully studied. For example, Bell (1919) wrote of *S. vulcanus* in India, "The eggs are laid anywhere…on practically any plant where there are ants of the genus *Crematogaster*—a particular species probably. The ants look after the little larvae from the first and these do not get on well without them." However, the results of our studies on Sri Lankan populations detailed below differ from those presented by Bell.

Spindasis vulcanus fusca (Moore, 1881). Common Silverline.

The immature stages of *S. vulcanus fusca* in Sri Lanka have not been described. In India, the final instar larva and pupa of *S. vulcanus* were described by de Nicéville (1890) and by Bell (1919), later quoted by Woodhouse (1949) and by Sidhu (2010). The results of our observations agree with these descriptions except for the following points: a) the larva is widest at S6–S7 (not S4), the constrictions between the segments are quite visible and the dorsal depressions are found only on S5–S8 (not S2–S11) (Fig. 5a); b) pupa (11 mm long, 4 mm wide) light green or black (Figs. 5b, c).

Egg laid singly on twigs, leaves and buds of the larval food plant, turns purplish-brown after a few days (Fig. 5d). 1st instar: newly emerged larva—head black and rather large, body light gray to pale yellow with two discontinuous dorsal grayish-brown lines on S7–S9 and darker colored patches of similar color subdorsally, S2–S4 and S10–S14 dark purple with long setae, in the remaining segments setae confined to the lateral margin (Figs. 5e, f). 2nd: almost identical to 1st except that body is light green and the subdorsal band is diffuse and a darker green, 3–4 small black subdorsal spots on each segment, S2–S4 and S10–S14 darker purple (Fig. 5g). 3rd: similar to 2nd but subdorsal band now with a whitish line at its center (Fig. 5h). 4th: similar to 3rd but dorsal line diffuse white, bordered by thin green line, with dark green circular depressions visible on S6–S7 (Fig. 5i). 5th: length 12 mm; green circular depressions visible on S5–S8, hairs around posterior segments end in small globular structures. We observed only the 4th and 5th instars in the field and these were attended by *Crematogaster* ants. A DNO and TOs were present in all instars although it is not certain if they were functional in the first 2 instars.

Duration of immature stages based on 3 specimens: egg (4 d); 1st instar (2 d); 2nd (3 d); 3rd (5 d); 4th (4 d); 5th (7 d); 2 days to pupate; pupa (8–11 d).

Members of the genus *Spindasis* are reported to use a wide range of larval food plants (Igarashi & Fukuda, 2000; Veenakumari *et al.*, 1997) and to have an association with a particular species of ant. Egg laying is assumed to be driven by the need to have the correct ant association. Since this study shows that the presence of ants is not a mandatory condition for oviposition or for normal development of the larva and pupa of *S. vulcanus fusca* under lab conditions, *ex-situ* breeding for this species for conservation purposes could be carried out successfully if necessary.

However, our field observations clearly indicate that females fly around and settle only on plants that have ants. At one location, we observed many females flying in and out of a large patch of the larval food plant over a 2-hour period from about 11am but no oviposition took place. The temperature at this time was around 32°C and ants were not active on the surface of the plants, but were present at the base of the plants amidst the leaf litter and dead wood. On further examination, several larvae and pupae were found inside tightly closed shelters which the larvae constructed by folding a few leaves together with silk. These shelters also contained 5–10 *Crematogaster* ants (species not identified) that were attending the larvae and pupae. No immature stages of the ant were found inside the shelter. The ants moved in a frenzied manner over the plant surface after the shelters were opened up (Fig. 5j).

A female kept in captivity laid eggs freely after 3 days without any ants and all the eggs hatched without ants. Some of these larvae developed normally without ants up to the 3rd instar at which point a local ant (*Tapinoma melanocephalum*) (Fig. 5k) invaded the lab and gained access to the containers holding the larvae and immediately attended to them. *T. melanocephalum* is a very small (1.5 mm) widespread, tropical ant that can become a household pest. It is fond of sugar and occasionally eats dead or live insects. It is not clear how the *Tapinoma* ants found the *Spindasis* larvae though they forage widely. There is no evidence of lycaenid larvae using volatile chemicals for long-range attraction of ants, and the interaction of ant and larva relies on substrate-borne vibration signaling and contact chemoreception (i.e. the ant needs to physically touch the larva to pick up a signal (K. Fiedler, pers. comm.). One of the larvae collected in the field (possibly 4th or 5th instar) did not have ants in its shelter but looked healthy and normal. Nevertheless it died 2 days later. It is possible that the ants kept away from this larva because it was diseased

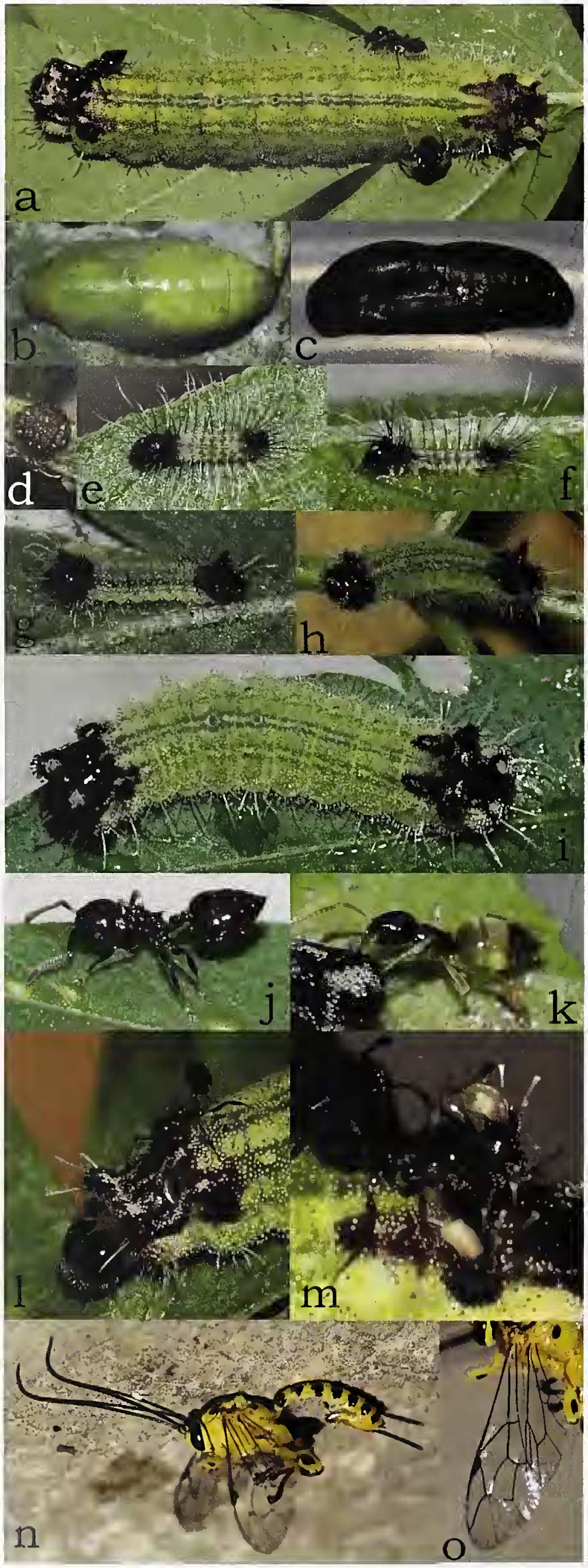


Figure 5. Early stages of *Spindasis vulcanus fusca* from Sri Lanka. **a)** Larva, fifth instar, attended by ants in the field. **b)** Pupa, green form, dorsal view. **c)** Pupa, black form, lateral view. **d)** Egg, day before hatching. **e)** Larva, first instar, dorsal view. **f)** Larva, first instar, lateral view. **g)** Larva, second instar, dorsolateral view. **h)** Larva, third instar, dorsal view. **i)** Larva, fourth instar, dorsal view. **j)** *Crematogaster* ant. **k)** *Tapinoma melanocephalum* attending larva in the lab. **l)** *Crematogaster* ant attending to anterior end of larva. **m)** *Crematogaster* ant attending to DNO; TOs everted. **n)** Ichneumid pupal parasitoid, female. **o)** Ichneumid pupal parasitoid, female, wing.

and was unable to produce the communication signals to maintain the association.

Both the field ants (*Crematogaster* sp.) and the lab ants (*T. melanocephalum*) were exceptionally excited around the larvae and ran about the shelter and container frantically, stopping frequently just behind the head at the junction of S2–S3 (Fig. 5l) and at the posterior end at the DNO. In the field and in the lab, the ants were periodically touched by the eversible tentacles of the TOs when they came to feed on the exudates of the DNO (Fig. 5m). It is not clear whether this behavior was to repulse the ants or to scent the ants for recognition. Ants attended the pupae as well.

The general habits of *S. vulcanus* in India described by de Nicéville (1890) apply to *S. vulcanus fusca* in Sri Lanka as well with some exceptions. The larva conceals itself by constructing a shelter which in the first 3 instars is not more than a partly folded up leaf. In the 4th and 5th instars the leaves or leaflets are brought together and held tightly with a small opening for the larva to exit to forage. The larva ventures out at night to feed but returns to its shelter during the day. At maturity, the larva pupates within the shelter constructed last. It does not seem to wander about in search of a place to pupate. The ants enter into the shelter built by the larva to attend to it. No ant nests were observed on the above-ground parts of the plant though the ants were observed moving up and down the stem of the plant to its base.

A parasitic ichneumoid wasp (family Ichneumonidae, species not identified) emerged from a pupa collected from the field (Fig. 5n, o). Another hymenopteran larval parasitoid was recorded in *S. vulcanus* in India (Sidhu, 2010).

Larval food plants: In Sri Lanka, d'Abrera (1998) reported that it fed on *Ixora clerodendron* [sic] though there is no such species. This record likely comes from confusing two records from India: that of de Nicéville (1890): "The larva in Calcutta feeds on *Clerodendron siphonanthus*"; and of Swinhoe (1911–1912): "Grote bred this species in Calcutta on *Ixora longifolia*." Woodhouse (1949) also quoted larval food plant information from Bell (1919) which is based on Indian sources. The current study showed for the first time that one of the larval food plants in Sri Lanka is *Cardiospermum halicacabum* (Sapindaceae), a plant completely unrelated to the genera *Ixora* (Rubiaceae) and *Clerodendrum* (Lamiaceae). The larvae feed on the leaves.

S. vulcanus fusca is widely distributed in the arid, dry and intermediate zones but scarce in the wet zone and hills. *Cardiospermum halicacabum* is common in the forests and waste lands in the moist and dry regions at lower elevations (Dassanayake, 1998). The distribution of this plant matches the distribution of the butterfly in that it has been found where the butterfly has been recorded. However, given the dependence of the butterfly on ants, its distribution is also likely constrained by the distribution of appropriate host ants. Since the members of the genus *Spindasis* tend to feed on a wide range of plants, it is likely that other larval food plants are used as well. For example, *S. v. vulcanus* has been reported in India as feeding on Rhamnaceae, Rubiaceae, Myrtaceae, Sapindaceae and Lamiaceae (Atluri *et al.*, 2012; Chowdhury *et al.*, 2009; Sidhu, 2010).

Spindasis schistacea (Moore, 1881). Plumbeous Silverline & *Spindasis nubilus* (Moore, [1887]). Clouded Silverline. Endemic.

The immature stages and larval food plants of these two species in Sri Lanka have not been described. In the course of this study, neither eggs, larvae nor pupae have been encountered. Adults of *S. schistacea* have been seen at a few widespread locations including Corbet's Gap, Kumbukgolla and Rambuk Oluwa (H. D. Jayasinghe, pers. comm.) and Elevankulam, Puttalam, Ritigala, Wasgamuwa and Riverston Knuckles (pers. obs.). Adults of *S. nubilus* have not been encountered though it has been historically reported from Giant's Tank, Jaffna and Elephant Pass.

Spindasis ictis ceylonica Felder, 1868. Ceylon Silverline. Endemic subspecies.

The immature stages and larval food plant of *S. ictis ceylonica* are described here for the first time.

Egg: pale green when freshly laid but turned dark brown within a day; disc-like, more or less flattened, not heavily sculptured like those of *S. vulcanus fusca*; micropylar end with a circular depression. 1st instar: Not recorded. 2nd, 3rd & 4th: similar to the 5th (Figs. 6a–d). 5th: Head black. Body salmon-colored, frosted in appearance, covered with minute white, black or dark brown funnel-shaped projections which give the larva its coloring and pattern; S3–S10 with subdorsal white, inverted-cone-shaped protuberances; dorsal line from S6–S9 with concentric white and gray rings with brown centers; outer edges of dorsal line reddish-brown, sometimes obscure; lateral line broad, wavy, irregular and dark reddish-brown; spiracular line similar but less wavy; S2 dark brown dorsally and projects forward to cover much of the head; dorsum of S2 suffused with minute funnel-shaped black projections anteriorly and white towards the center and back; S3 black and densely packed with minute funnel-shaped projections; S11–S14 with a continuous black patch dorsally extending to the subdorsal line; S11 with a well-developed DNO; S12 with a pair of eversible TOs placed within the center of a cone-shaped projection that is rimmed with 5–6 clubbed filaments; between the TOs, four similar, shorter, clubbed filaments; anal plate light gray with minute dark-colored depressions and connected to the flange by 5 irregular lines that radiate out from the periphery of the gray center; numerous white filaments of even width extend out from the body along the flange and just below (Fig. 6d). Pupa: similar to that of *S. vulcanus fusca* (Fig. 6e). *S. ictis ceylonica* is multibrooded: larvae have been found at the same location in June, July and November. Duration of immature stages (based on observations of 3 specimens): 4th (11 d); pupa (9–11 d).

Larval food plants: One of the larval food plants in Sri Lanka is *Acacia eburnea* (Fabaceae-Mimosoideae); the larvae fed on the leaves. The larvae were found in the field in the company of *Crematogaster* ants (species not identified) at two locations: at Arippu (8°48'14.4"N, 79°56'22.6"E, 1 m asl) on the west coast in the Mannar district (Fig. 6f) and at Chundikulam (9°28'40"N, 80°35'38"E; 1 m asl) in the Jaffna district on the northeast coast (Fig. 6g).

The *Crematogaster* ants were small (3.5 mm long), black and reddish-brown. They formed colonies inside the paired thorns of *Acacia eburnea* (Fig. 6h), which are usually fused at the base. The thorns are filled with a corky material even when mature. It is likely the ants that remove the interior pith to create space inside the thorns as no hollow thorns were found without an ant entrance hole. Each colony comprises about 50–80 ants with eggs, larvae and pupae in the largest thorns of the Arippu population in which the largest thorns measured 80 mm in length and 11 mm in diameter at the base. At Chundikulam, the colony comprises about 20–25 in the largest thorns which measure 60 mm in length and only 7 mm in diameter at the base. The ants enter and exit from the thorns through a small hole (one hole per paired thorn, 1–2 mm in diameter) that is placed almost anywhere on the thorn but usually near the

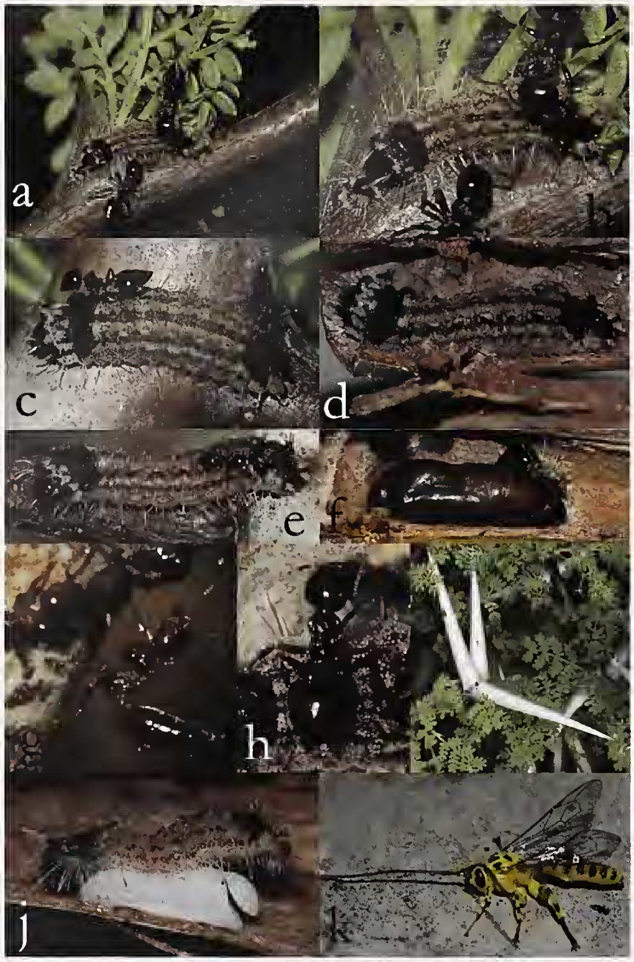


Figure 6. Early stages of *Spindasis ictis ceylonica* from Sri Lanka. **a)** Larva, second instar, dorsal view, with its larval nest and *Crematogaster* ants. **b)** Closeup of second instar larva. **c)** Larva, third instar, dorsal view. **d)** Larva, fourth instar, dorsal view. **e)** Larva, fifth instar, dorsolateral view. **f)** Pupa inside hollow thorn, lateral view. **g)** *Crematogaster* ant from Arippu. **h)** *Crematogaster* ant from Chundikulam. **i)** Paired thorns of *Acacia eburnea* with ant nest entrance hole visible in the center. **j)** Early instar larval skin with parasitoid pupa below from which the parasitoid has emerged. **k)** Ichneumid parasitoid, male, emerged from pupa.

base. The ants were observed feeding on the glands on the petiole of *A. eburnea* and on dead insects at the base of the plant. They are not aggressive though they swarmed out when their colony was disturbed. Their sting is very mild.

S. ictis ceylonica females usually oviposited next to the hole of the ant nest in the thorn. On hatching, the larva consumed part of the eggshell. Usually one or two larvae, often of different instars, were found inside the thorns with ants attending them, and sometimes with one or two pupae as well. Larvae were observed exiting the ant nest near sundown and during heavy cloud cover. Early instar larvae were observed making nests using silk to bind a few leaves together or with silk at the fork of small twigs, particularly when about to molt (Fig. 6a). The ants attended the *Spindasis* larvae assiduously, and fed on the fluid exuded by the DNO on the 11th segment. The ants were also active on the dorsum of S2–S3 from where they appeared to obtain some nutrition. The larva had the habit of quickly everting its TOs and touching the ants with the everted filaments when the ants were close to the DNO or TOs.

As the larva grew bigger, it made the entrance to the ant nest larger by chewing away the sides of the hole but the ants sometimes glued small pieces of chewed material to make the hole smaller again, only to have it enlarged again by the larva. The partition between the paired thorns eventually disappeared, perhaps chewed away by the larvae and/or ants, thus expanding the space available within. In the field, we found pupae inside hollow thorns with their heads pointing towards the entrance hole, usually within 1 cm of the hole. Usually one pupa was found per thorn but occasionally two, one on either side of the ant entrance hole. In the lab, the larvae pupated inside hollow thorns that were provided to them.

In the Chundikulam population, an early instar larva was found that had been parasitized though the parasitoid had already emerged (Fig. 6i) and a parasitoid wasp (family Ichneumonidae, species not identified) emerged from a pupa (Fig. 6j). Neither larval nor pupal parasitoids were found in the Arippu population.

S. ictis ceylonica is common in the plains of the dry and arid zones. It is also found in the drier hills of the eastern slopes up to about 1500 m asl in the Uva province in places such as Haputale and Bandarawela where the largest specimens and only the dry season form occur.

Acacia eburnea is a shrub or small tree found in very dry areas along the northwest coast from Anavilundawa to Jaffna and thence along the northeast coast to Yala in the southeast corner of the island (Dassanayake, 1980). The plant is absent in the drier hills of the Uva province and the inland areas of the dry zone. *S. ictis ceylonica* must therefore feed on other plants in these areas since the butterfly is not known to take part in flights and so must be breeding there. The distribution of the *Crematogaster* ant is unknown.

Spindasis elima fairliei Ormiston, 1924. Scarce Shot Silverline. Endemic subspecies.

The immature stages and larval food plant of *S. elima fairliei* are described here for the first time.

Egg: similar to that of *S. ictis ceylonica* (Figs. 7a, b). 1st instar: Head shiny black. Body light purplish-red with a faint white dorsal line; S2 large, rounded on the sides and slightly raised above other segments with a rounded, dark shiny dorsal patch; S3 and S4 dark on the dorsum; S4–S10 with whitish subdorsal diffuse spots that become smaller posteriorly; S12 with a short dark transverse band; S13 with a circular dark area on the dorsum; S2–S3 and S11–S14 with long black setae with white tips; S4–S10 with short, black setae arranged in transverse bands (Fig. 7c). 2nd: similar to the 1st except for the following: body slightly darker purplish-red covered with minute funnel-shaped projections; obscure white lateral line; large black patch on dorsum of S2 more prominent; DNO on S11 more clearly marked and fringed with 2–3 black filaments; S12 with a pair of TOs between which are two rows of black, slender, oblong filaments; setae absent; body covered with black club-shaped projections with brownish tips (Fig. 7d). 3rd: similar to the 2nd but in addition, minute, short-stalked, white, funnel-shaped projections on S2–S12; dorsal shield on S2 well defined, very dark and raised with a ridge along the dorsal line; S3 and S11 darker dorsally than the remaining segments except S2 (Fig. 7e). 4th: similar to the 3rd (Fig. 7f). 5th: similar to the 4th but with the following differences: body paler in colour—a light brownish-purple and more heavily speckled with funnel-shaped projections so that the larva appears frosted; translucent or white filaments along the edge of flange; spiracles light brown and indistinct (Fig. 7g). Pupa: similar to that of *S. vulcanus fusca*; 11 mm long, 3.5 mm wide (Fig. 7h). Duration of immature stages (based on observations of 4 specimens): 1st instar (4 d); 3rd (5–7 d); 4th (14 d); 5th (20 d); pupa (11 d).

Larval food plants: One of the larval food plants in Sri Lanka is *Acacia eburnea* (Fabaceae-Mimosoideae); the larvae fed on the leaves. The larvae were found in a field at Arippu, Mannar in the company of a species of *Crematogaster* ant that is yet to be identified. *S. ictis ceylonica* larvae were also found in the company of the same ant on the same bush and sometimes even within the same thorn.

See *S. ictis ceylonica* for a description of the ants, the behavior of the larvae and the distribution of *A. eburnea*. The only difference noted was that *S. elima fairliei* females were less discriminating and oviposited on any part of the plant as long as the ants were active nearby.

S. elima fairliei is found in the northern province and along the northwest coast of the arid zone. A few stray south along the northwest coast into the dry zone as far south as Anavilundawa. It inhabits the thorn scrub of the arid zone and the scrub jungle of the dry zone. It is not rare but is often mistaken for *S. ictis ceylonica*.

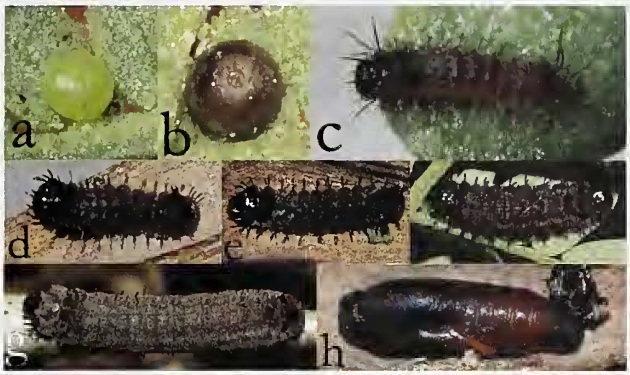


Figure 7. Early stages of *Spindasis elima fairliei* from Sri Lanka. **a)** Egg, first day. **b)** Egg, second day. **c)** Larva, first instar, dorsal view. **d)** Larva, second instar, dorsal view. **e)** Larva, third instar, dorsal view. **f)** Larva, fourth instar, dorsal view. **g)** Larva, fifth instar, dorsal view. **h)** Pupa, dorsolateral view.

We have recorded the larvae of *S. elima fairliei* feeding only on *A. eburnea* and have found the plant wherever the butterfly has been recorded. However, given the propensity for larvae of the genus *Spindasis* to be polyphagous, there may be other larval food plants.

Spindasis lohita lazularia (Moore, 1881). Long-banded Silverline.

The final instar larva and pupa of *S. lohita lazularia* in Sri Lanka were described briefly by Moore (1880) and d'Abrera (1998) while Green (1902) briefly described its association with *Crematogaster* ants. Woodhouse (1949) quoted the description of the immature stages of *S. lohita* in India from Bell (1919). The immature stages of other subspecies of *S. lohita* in other countries have been fairly well documented (e.g. in Taiwan by Igarashi & Fukuda, 2000; in Singapore by H. Tam, 2010) and its larval food plants recorded (e.g. in the Andamans by Veenakumari *et al.*, 1997; in Malaysia by K. Fiedler, pers. comm.). *S. lohita* is a prime example of an obligate association with *Crematogaster* (in Malaysia: *C. dohrni artifex*), coupled with wide-ranging polyphagy (K. Fiedler, pers. comm.). In the course of this study, neither eggs, larvae nor pupae have been encountered but adults have been seen at several locations in all climatic zones including Atweltota, Elevankulam, Monaragala and Matale (H. D. Jayasinghe, pers. comm.) and Knuckles, Morningside and Puttalam (pers. obs.).

Conclusions

The immature stages of the genus *Spindasis* in Sri Lanka have been incompletely documented and many assumptions have been made particularly about the relationships of the larvae and pupae to the ants. These assumptions need to be revisited in light of the findings of the studies presented here. The life-cycles of all species deserve to be studied more carefully and in-depth. Similarly, with the exception of some species of *Spindasis* from Africa, the life cycles of other Asiatic *Spindasis* need to be better studied since only *S. lohita*, *S. syama* and *S. takanonis* are reasonably well covered.

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